

Habitat preferences of four sympatric species of shrews

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Habitat preferences were studied in a shrew community of two semiaquatic species, *Neomys anomalus* Cabrera, 1907 and *N. fodiens* (Pennant, 1771), and two terrestrial species, *Sorex araneus* Linnaeus, 1758 and *S. minutus* Linnaeus, 1766, in a study area (5600 m²) alongside a small stream in Białowieża Forest (E Poland). Preferences were estimated by relating frequency of captures with macro- and microhabitat characteristics of trapping points. Distance to the stream and ground wetness appeared to be more important than macrohabitat and plant cover in separation of habitat niches. *N. fodiens* was trapped at places significantly wetter and closer to the stream than the three other species, *N. anomalus* was captured at places wetter and closer to the stream than *S. araneus* and *S. minutus* was trapped closer to the stream than *S. araneus*. Habitat preferences of these species reflected vertical segregation in their foraging. The interspecific overlaps in habitat preferences were lowest between *N. fodiens* and the two *Sorex* species and highest between *N. anomalus* and *S. araneus* and between the two *Sorex* species. An inverse relationship between the breadths of the trophic and habitat niches of the shrews appeared: the greatest trophic specialist *S. minutus* had the broadest habitat niche, whereas the greatest trophic generalist *N. fodiens* had the narrowest habitat niche. High interspecific overlaps in habitat preferences and little overlaps in spatial distribution suggest that the separation of ecological niches of these four species in the study site reflects other mechanisms in addition to habitat preferences.

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Introduction

Interspecific competition still focuses the attention of ecologists. Separation of habitat niches is one of the most important mechanisms diminishing competition and allowing coexistence of ecologically similar species of mammals (Schoener 1974, Morse 1980, Neet and Hausser 1990). For shrews, studies of the habitat preferences of individual species or pairs of competing species are now being replaced by investigations of the multi-species communities (Sheftel 1994, Churchfield *et al.* 1997, Castián and Gosálbez 1999). Similarly, simple interspecific comparisons of shrews at the macroscale have given way to analyses of subtle relationships between microhabitat preferences and foraging behaviour or body size (Dickman 1988, Ellenbroek and Hamburger 1991, Churchfield 1994, Churchfield and Sheftel

1994, Ohdachi 1995, Rychlik 1997). Meanwhile, shrews have proved to be excellent models to verify theories and hypotheses on coexistence, competition and optimal foraging (Barnard and Brown 1981, Churchfield 1991b, Kirkland 1991, Hanski 1992, 1994, Vogel *et al.* 1998).

Shrews often display high levels of interspecific overlap of habitat niches (Spencer and Pettus 1966, Brown 1967, Wrigley *et al.* 1979, Churchfield *et al.* 1997, Castián and Gosálbez 1999). However, certain segregation of habitat niches is usually observed. It relied on selection of places differing with regard to the following microhabitat factors: density and type of plant cover, distance to water, soil wetness or water level, soil type or richness, litter layer, and quantity of woody debris (Spencer and Pettus 1966, Brown 1967, Hawes 1977, Wrigley *et al.* 1979, Terry 1981, Neet and Hausser 1990, Sheftel 1994, Shvarts and Demin 1994, Dickman 1995, Lee 1995, Castián and Gosálbez 1999). In some cases separation of habitat optima or mutual habitat exclusion has been observed (Hawes 1977, Neet and Hausser 1990, Sheftel 1994).

In the present study, the shrew community of four species coexisting in wet habitats along a small stream was analysed. The shrew community included two semiaquatic species, *Neomys anomalus* Cabrera, 1907 and *N. fodiens* (Pennant, 1771), and two terrestrial species, *Sorex araneus* Linnaeus, 1758 and *S. minutus* Linnaeus, 1766. This is the first study of habitat preferences in a shrew community including two semiaquatic species.

The macrohabitat preferences of European shrews are well known. The two *Neomys* species live mainly along small water courses and ponds, and in swamps and marshy meadows; the two *Sorex* species are most abundant in thick grass, bushy scrub and deciduous woodland (Dehnel 1950, Aulak 1970, Pucek 1981, Churchfield 1991a). However, there are still some discrepancies. For example, according to Churchfield (1991a), *S. minutus* prefers grassland over woodland, whereas according to Pucek (1981), *S. minutus* lives mainly in deciduous and mixed forests. *S. minutus* tends to select wetter biotopes than *S. araneus* in NE Poland, but in other regions the opposite is the case (Pucek 1981). In Białowieża Forest macrohabitat preferences of these two species differ: *S. araneus* prefers damp oak-hornbeam forest and spruce and pine forests, whereas *S. minutus* is most frequent in sedge swamps and bog pine forests (Aulak 1970).

The microhabitat preferences of the four species are poorly investigated. It can be assumed that microhabitat preferences of shrews are determined largely by their body size, foraging modes and food preferences (Yoshino and Abe 1984, Ellenbroek and Hamburger 1991, Churchfield 1994, Churchfield and Sheftel 1994, Ohdachi 1995, Churchfield *et al.* 1997). Comparative studies of the foraging behaviour of *S. araneus* and *S. minutus* have suggested vertical segregation of their foraging microhabitats, with *S. araneus* foraging mainly in litter and the upper layer of the soil and *S. minutus* foraging on the ground surface and low vegetation (Churchfield 1980, Dickman 1988, Ellenbroek and Hamburger 1991). These differences have been demonstrated by examination of diets and prey preferences

(Pernetta 1976, Butterfield *et al.* 1981, Bauerova 1984, Churchfield 1994, Rychlik and Jancewicz 1996).

Foraging behaviour of *N. fodiens* and *N. anomalus* has been examined under many experimental conditions (Ruthardt and Schröpfer 1985, Rychlik and Jancewicz 1996, Rychlik 1997, 1999a, b, Vogel *et al.* 1998). It has been found that (1) *N. fodiens* is able to forage in both deep and shallow water, whereas *N. anomalus* can only forage successfully in shallow water; (2) dense vegetation cover is more important for *N. anomalus* than *N. fodiens*. Diet analyses have supported these conclusions for *N. fodiens* (eg Wolk 1976, Kuvikova 1985, DuPasquier and Cantoni 1992, Castián 1995), but only few data on the diet of *N. anomalus* are available (Niethammer 1977, 1978, Kuvikova 1987, Ramalhinho 1995). Nevertheless, these findings, along with some information on the microhabitat preferences of these two species (Niethammer 1977, 1978, Schröpfer 1985, Andéra 1993, 1995, Ramalhinho 1995), led Rychlik (1997) to put forward the following hypothesis about microhabitat preferences of the two water shrews: *N. fodiens* prefers sites with direct access to deep water and steep, structured banks, whereas *N. anomalus* prefers places with access to shallow water under dense vegetation cover. That is, as for *Sorex*, some vertical segregation of foraging microhabitats is expected also in the two *Neomys* species.

Thus, the aims of the present field investigations were: (i) to describe habitat preferences of the four shrew species in the community under study, (ii) to verify the hypothesis about differences in microhabitat preferences between *N. fodiens* and *N. anomalus*, and (iii) to test the hypothesis about vertical segregation of foraging microhabitats among the four species.

Interspecific differences at the micro- rather than macroscale are expected in habitat preferences of small mammals (Seagle 1985). However, because coexisting species may overlap extensively in one niche dimension and only slightly in another, more than one dimension of habitat niches should be examined (Schoener 1974). Therefore, one macrohabitat factor (plant community) and three microhabitat factors (plant cover type, distance to the stream and wetness of the ground) were analysed in the present study. Significant differences in habitat preferences of small mammals over successive years indicate that studies on habitat preferences have to continue for a considerable period (Aulak 1970, Raczyński *et al.* 1983). Therefore, data from a 9-year-period (1988–1996) are analysed in the present study.

Material and methods

Habitat analysis of the study area

The study area (in size 80 × 70 m, 5600 m²) was localised in the valley of Narewka river in forest compartment 426 of the Białowieża Forest (E Poland). An asphalt road was 3 m away from the north-eastern side of the plot and a stream crossed through the plot (Fig. 1a).

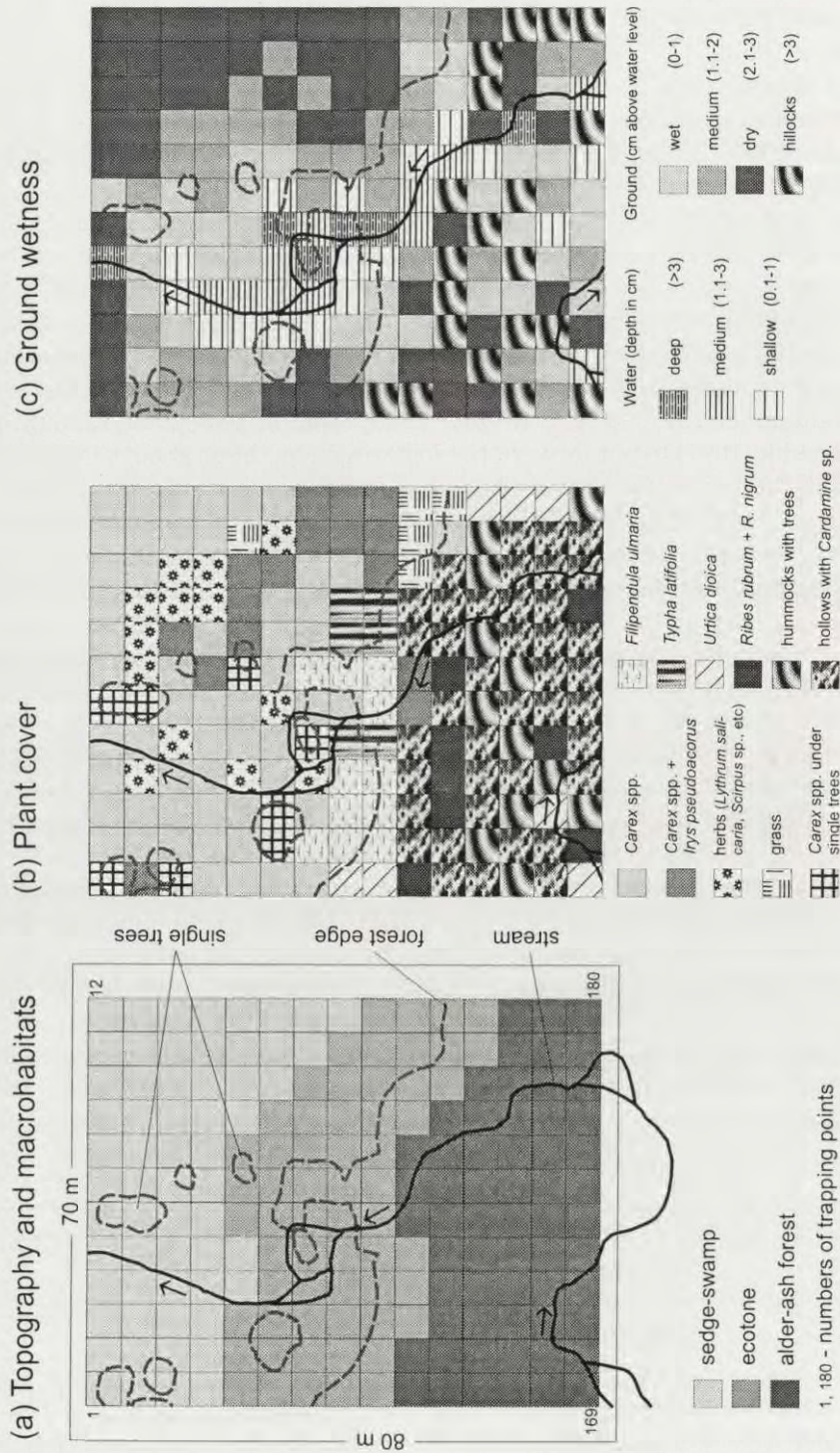


Fig. 1. Size and topography of the study area and position of different habitat features.

The area included three macrohabitats: tussock-sedge swamp (*Caricetum appropinquatae* from alliance *Magnocaricion*), streamside alder-ash forest (*Circaeo-Alnetum* from alliance *Alno-Padion* according to Faliński 1986) and the ecotone between them. [The term 'macrohabitat' is of course not at a global scale (as tundra, taiga, etc) in this paper, but it is used for comparison with features analysed at a microscale]. The ecotone was determined arbitrary in such a way that each macrohabitat was represented by an equal area, it was represented on both sides of the projections of tree crowns at forest edge and it comprised patches of *Filipendula ulmaria* (Fig. 1).

During the summers of 1990–1992 the following characteristics were mapped: course of the stream, projections of tree crowns in sedge swamp and at forest edge, position of patches of dominating herbaceous and shrubby plants, position of standing tree trunks, stumps and fallen logs, and localisation of hummocks and hollows. For each trapping point the minimal distance to the stream was measured and, following the method of Tast (1966), the category of vegetation cover prevailing 1 m around the point was determined. Plant species or genera which constituted $\geq 40\%$ of cover within a given patch were considered. Eleven categories of plant cover were distinguished and their distribution is shown in Fig. 1b.

Since 1990, simultaneously with each trapping session, mean wetness of the ground and the depth of stagnant or flowing water (if present) 1 m around each trapping point were estimated at midday. The average ground wetness and water level at each trapping point were calculated for all 19 trapping sessions and seven categories were distinguished (Fig. 1c). The depth of the stream usually ranged from 3 to 20 cm and changed according to precipitation.

Trapping procedure

The study plot included 180 trapping points distributed in a grid at 5-m-spacing. Trapping points were in the centre of each square shown in Figs 1 and 2. Usually wooden-box live-traps were used, except in 1988 when metal-cone pitfalls were used instead and in 1993–1994 when both types of traps were employed. Minced meat was always put as the bait into pitfalls and into box live-traps in 1993–1994. Usually, traps were open 24 hours non-stop and patrolled every 4–5 hours. In 1988, all *N. anomalus*, *N. fodiens* and *S. araneus*, and in 1993–1994 all shrews, were taken to the laboratory. All other animals captured were released at the point of capture.

Between 1988 and 1996, there were 19 trapping sessions. These lasted from 4 to 15 days (mean 8.7 days, median 10 days) and took place between June and September, except one trapping session in October 1988 and one in May 1990. Total trapping effort was 435 882 trap-hours (86%) for box-traps plus 72 273 trap-hours (14%) for pitfalls.

Data analysis

Particular trapping sessions differed with regard to number of trapping points used, number of traps (one or two) set at one point and hours the traps were open. Therefore, the total numbers of captures in each trapping point were standardised, ie divided by the total numbers of hours the point was open and the numbers of traps set at that point. Next, the values obtained were converted into percentages (shown in Fig. 2).

Preferences for all habitat features were estimated and expressed by Ivlev's electivity index (Jacobs 1974). Interspecific differences in habitat preference were estimated by interspecific overlap according to a formula modified from Pianka (1973). Two-dimensional factor space analysis (Sheftel 1994) was used to assess simultaneously the influence of wetness and distance to the stream. Habitat niche breadths (indices of habitat diversity) were estimated according to the formula given by Churchfield *et al.* (1997). Mann-Whitney Two Sample (GraphPAD InStat 1.13 1990), Wilcoxon Signed Ranks (SYSTAT 5.01 1992) and Goodness of Fit tests were used in statistical analyses. See Rychlik (2000) for more details on methods.

Results

In total, 2216 captures (including recaptures) of 14 mammal species were recorded. This included: 179 captures (152 in box-traps + 27 in pitfalls) of *N. anomalus*, 343 (282+61) of *N. fodiens*, 610 (418+192) of *S. araneus*, and 133 (49+84) of *S. minutus*. The dominant rodents were *Clethrionomys glareolus* (530 captures) and *Microtus oeconomus* (313).

The spatial distributions of all shrew captures are shown in Fig. 2 as percentages of captures recorded at particular trapping points. For *S. araneus* this

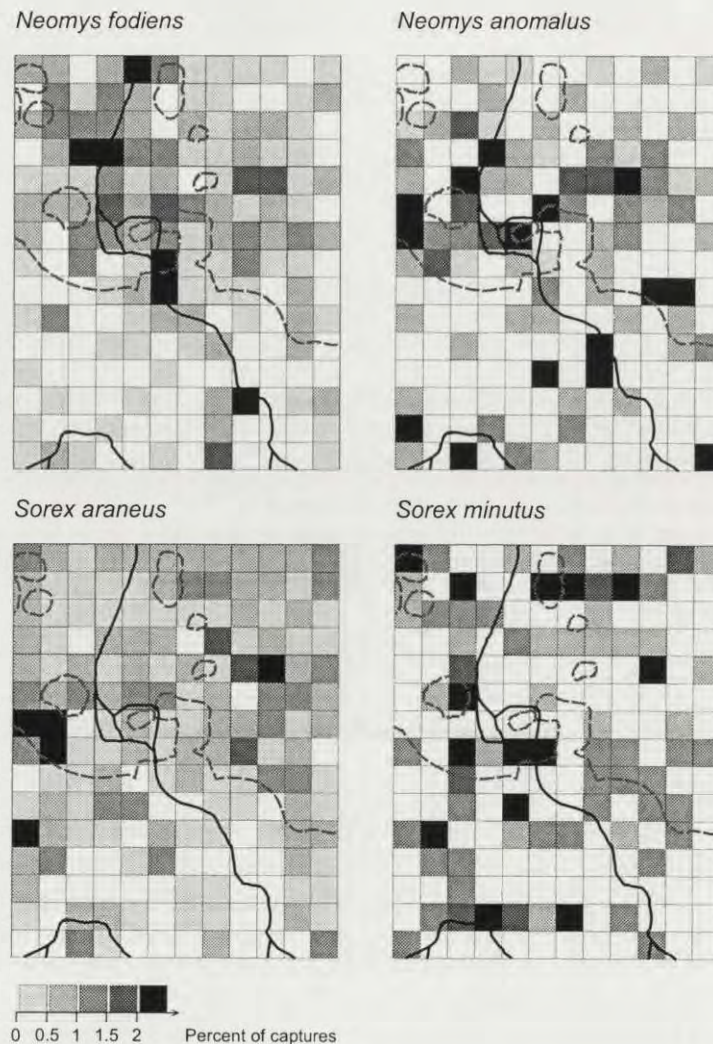


Fig. 2. Spatial distribution of all captures of the four shrew species.

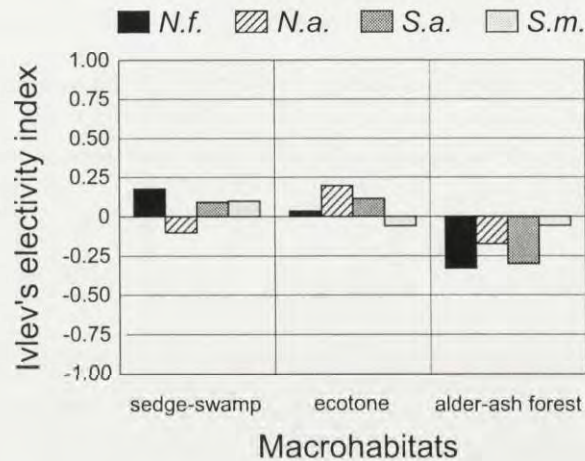


Fig. 3. Comparison of macrohabitat preferences of the four shrew species, expressed by Ivlev's electivity index. *N.a.* - *Neomys anomalus*, *N.f.* - *N. fodiens*, *S.a.* - *Sorex araneus*, *S.m.* - *S. minutus*.

distribution was very uniform, for *S. minutus* it was very clustered and for the two *Neomys* species it was intermediate with *anomalus* more clustered than *fodiens*. *N. fodiens* was more frequent in sedge-swamp (48% of captures) than in the ecotone (35%) and forest (17%) (Figs 1a and 2). *N. anomalus* was mainly trapped in the ecotone (50%) and it was less frequent in sedge-swamp (27%) and alder-ash forest (23%). In *N. fodiens* most points of high trappability were close to the stream, whereas in *N. anomalus* they were some distance from the stream. *S. araneus* was more frequent in sedge-swamp (40%) and the ecotone (42%) than in forest (18%), and places of high trappability were quite far from the stream. *S. minutus* was rather equally frequent in all macrohabitats (40, 30 and 30% respectively for swamp, the ecotone and forest), and some places of high trappability of this species were close to the stream.

The comparison of macrohabitat preferences (Fig. 3) showed that the four species displayed neither strong preference nor avoidance of sedge-swamp and the ecotone. However, *N. anomalus* displayed a tendency to avoid sedge-swamp and to prefer the ecotone. Alder-ash forest was avoided by *N. fodiens* and *S. araneus*. In contrast, *S. minutus* displayed some tolerance for this macrohabitat.

Analysis of plant cover preferences (Fig. 4) revealed that *N. fodiens* preferred *Carex* patches but avoided grass patches and all forest microhabitats. *N. anomalus* preferred places with *Carex* spp. under single trees and hummocks with trees but avoided all other types of plant cover in forest. *S. araneus* preferred places with *Carex* spp. under single trees and avoided all forest microhabitats except hummocks with trees. Like *N. anomalus*, *S. minutus* preferred places with *Carex* spp. under single trees and hummocks with trees. But *S. minutus* preferred patches of *Typha latifolia* which were rather avoided by *N. anomalus*.

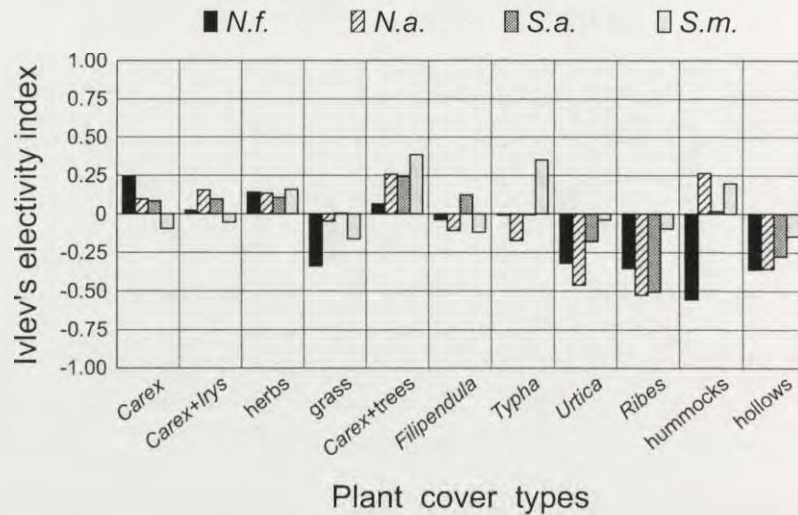


Fig. 4. Comparison of plant cover preferences of the four shrew species.

N. fodiens preferred places at a distance of 0–0.5 m from the stream (Fig. 5). It was more frequent here than *N. anomalus*, whereas the two *Sorex* species tended to avoid such places. *N. fodiens* avoided places at distances greater than 5 m from the stream. *N. anomalus* displayed a tendency to prefer places directly at the stream and at distances 10.1–15 m from the stream but rather avoided all places at distances >15 m. *S. araneus* tended to avoid all places closer than 10 m from the stream and to prefer all places at distances >10 m. In contrast, *S. minutus* preferred places only 0.6–2 m away from the stream and avoided places at distances >20 m.

Fig. 6 shows that both *Neomys* species preferred places with water of depth 1.1–3 and >3 cm and both avoided hillocks. *N. fodiens* avoided all places above the water level. *S. araneus* tended to prefer only dry places and to avoid shallow water and hillocks. *S. minutus* avoided places with water 1.1–3 cm deep.

Interspecific overlaps (Table 1) in the spatial distribution of captures were significantly lower (mean \pm SE = 40.3 \pm 5.9%) than in preferences to different features of habitat (91.3 \pm 1.6%; Wilcoxon test: $Z = 2.2$, $p = 0.03$). The highest overlaps in both capture distribution and mean microhabitat preferences were between *N. anomalus* and *S. araneus*. These species overlapped considerably also in macrohabitat preferences. The overlaps between the two *Sorex* species were high in all categories. The lowest overlaps were: between *N. anomalus* and *S. minutus* in capture distribution, between *N. anomalus* and *N. fodiens* in macrohabitat preferences, and between *N. fodiens* and *S. minutus* in microhabitat preferences. *N. fodiens* and *S. araneus* were very similar in macrohabitat and plant cover preferences but they clearly differed in preferences relating to distance to the

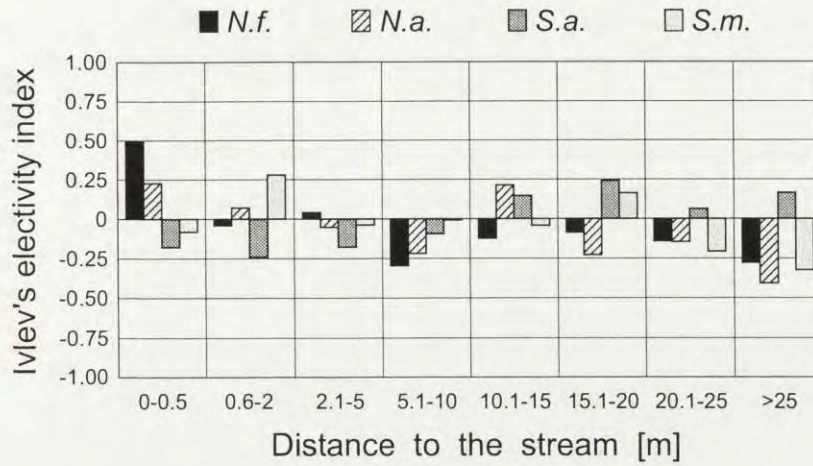


Fig. 5. Comparison of preferences in distance to the stream of the four shrew species.

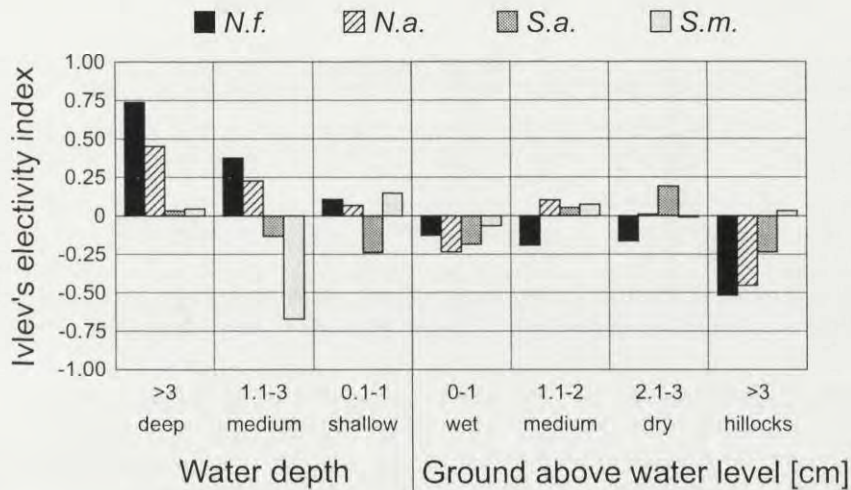


Fig. 6. Comparison of preferences in ground wetness of the four shrew species.

stream and ground wetness, so the mean overlap between their microhabitat preferences was low.

Generally, the interspecific overlaps in all habitat categories were quite high (Table 1). However, the overlaps in distance to the stream and wetness were significantly lower than in macrohabitat and plant cover (Wilcoxon test: $Z = 2.9, p = 0.004$). This fact suggests that the first two factors were more important than the two latter in reducing overlaps in capture spatial distribution.

Table 1. Comparison of interspecific overlaps (in %) in capture space distribution of shrews, in their preferences to different features of habitat, and in mean microhabitat preferences. *N.a.* – *Neomys anomalus*, *N.f.* – *N. fodiens*, *S.a.* – *Sorex araneus*, *S.m.* – *S. minutus*.

Feature	<i>N.a./N.f.</i>	<i>N.a./S.a.</i>	<i>N.a./S.m.</i>	<i>N.f./S.a.</i>	<i>N.f./S.m.</i>	<i>S.a./S.m.</i>
1. Capture distribution	39.4	63.9	24.3	43.2	26.0	44.8
2. Macrohabitat	91.4	96.6	91.5	98.7	96.7	96.0
3. Plant cover	95.9	99.0	94.4	97.1	87.4	95.2
4. Distance to stream	87.1	92.7	89.7	75.3	79.5	92.9
5. Ground wetness	89.3	95.4	95.3	78.7	81.6	94.3
6. Mean for rows 3–5	90.8	95.7	93.1	83.7	82.8	94.1

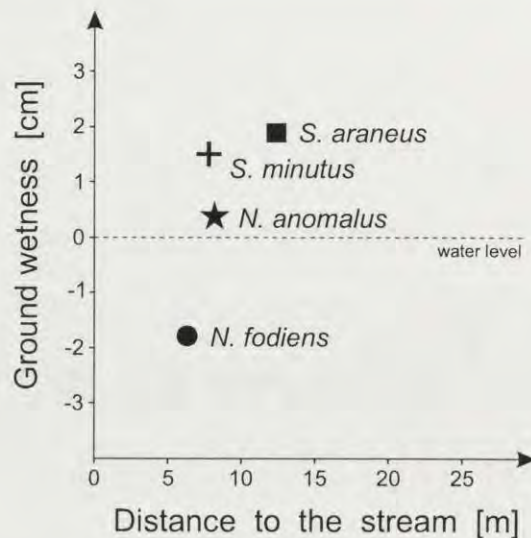


Fig. 7. Distinction between the four species of shrews with regard to mean distance to the stream and mean ground wetness (positive values – height of ground above water level, negative values – depth of water) at places they were captured, plotted in the two-dimensional factor space.

Therefore, mean distance to the stream and mean wetness at places of captures were chosen to show the habitat preferences of these species in the two-dimensional factor space (Fig. 7). The values for *N. fodiens* differed significantly from those for the three other species (Mann-Whitney test: $U = 4529.5$ to $16\,993.0$, $p < 0.001$ to $p < 0.03$ for distance to the stream and $U = 1950.5$ to $12\,329.0$, $p < 0.001$ for wetness). Also the differences between *N. anomalus* and *S. araneus* were significant ($U = 12\,881.5$, $p < 0.001$ and $U = 8840.5$, $p < 0.001$, respectively). The two *Sorex* species did not differ with regard to mean wetness of capture sites ($U = 3964.0$, $p = 0.29$), but *S. minutus* was trapped significantly closer to the stream

Table 2. Comparison of niche breadths of the four shrew species with regard to different features of habitat and in mean microhabitat niches.

Feature	<i>N. fodiens</i>	<i>N. anomalus</i>	<i>S. araneus</i>	<i>S. minutus</i>
1. Macrohabitat	1.02	1.04	1.04	1.09
2. Plant cover	1.73	1.98	2.03	2.17
3. Distance to stream	1.85	1.84	1.91	1.92
4. Ground wetness	1.86	1.78	1.59	1.70
5. Mean for rows 2–4	1.81	1.87	1.84	1.93

than *S. araneus* ($U = 3584.0, p < 0.001$). The differences between *N. anomalus* and *S. minutus* were insignificant ($U = 3310.5, p = 0.85$ for distance to the stream and $U = 1413.0, p < 0.12$ for wetness), but *S. minutus* tended to select drier places than *N. anomalus*. Thus, this analysis also showed that *N. fodiens* was captured in wet places close to the stream, *S. araneus* was captured in dry places distant from the stream, and *N. anomalus* and *S. minutus* were trapped in places with intermediate features.

Generally, breadths of macrohabitat niches were less differentiated than those of microhabitat niches (Table 2). Niche breadths for plant cover were the most variable, and those for ground wetness were second. Microhabitat niches were the narrowest in *N. fodiens* and the broadest in *S. minutus*. Niche breadths of *N. anomalus* and *S. araneus* were very similar and intermediate to the two other species. *S. araneus* was rather unselective with regard to plant cover but it tolerated very narrow range of ground wetness.

Discussion

It could be suggested that variable trapping procedure was a shortcoming of this study. However, this is unlikely to be important for several reasons: (1) different trapping efforts at particular points and habitat categories were taken into account by the standardisation of data on trapping success, (2) 72.5% of captures of all shrews were recorded during the 11 'regular' trapping sessions (in 1990–1992 and 1996) and only 27.5% during the remaining 8 sessions, and (3) in spite of variable trapping procedures, distinct interspecific differences in habitat preferences have been found in other studies (Spencer and Pettus 1966, Yalden *et al.* 1973, Wrigley *et al.* 1979).

Pitfall traps have usually been found to be more effective than box-traps in trapping shrews (eg Croin Michielsen 1966, Maddock 1992), especially the small species (Brown 1967, Shvarts and Demin 1994). In the present study, the ratio of box-trap to pitfall trapping effort was 6.0 (I used mostly box-traps to collect faeces of shrews, which was impossible from pitfalls). The ratios of box-trap to pitfall

trapping success did not differ significantly from 6.0 in *N. anomalus* (5.6), *N. fodiens* (4.6) and *S. araneus* (2.2), but was significantly lower in *S. minutus* (0.6; Goodness of Fit test: $G = 5.128, p < 0.05$). This suggests that my box-traps were not sensitive enough for *S. minutus* and its space use was underestimated. Therefore, the conclusions on habitat preferences of this species should be considered with caution.

Interspecific differences

The shrews studied did not display clear differences in macrohabitat preferences. This fact is consistent with the prediction of Seagle (1985) and similar to the results of Yudin (1962) and Casti n and Gos lbez (1999). In contrast, Aulak (1970), Sheftel (1994) and Churchfield *et al.* (1997) found that *N. fodiens* preferred different macrohabitats from *S. minutus* and *S. araneus*. But in my study only three very similar macrohabitats (eg with regard to ground wetness) were analysed, whereas in the studies of Aulak, Sheftel and Churchfield *et al.* 7–11 very variable biotopes were compared, which surely allowed shrews to display greater differentiation in their preferences.

Avoidance of alder-ash forest by the *S. araneus* found in the present study is in contrast to many observations of its preference to different types of woodland (Yudin 1962, Yalden *et al.* 1973, Schr pfer 1990, Shvarts and Demin 1994), and especially to earlier findings that common shrews were particularly frequent in alder forest (Raczyński *et al.* 1983) and riparian alder-spruce forest (Churchfield *et al.* 1997). Yalden *et al.* (1973) captured no pigmy shrews in woodland or woodland-edge, whereas I captured 30% of *S. minutus* in forest. Similarly, this species has been found to be frequent in different kinds of forest throughout the Palearctic (Yudin 1962, Aulak 1970, Raczyński *et al.* 1983, Schr pfer 1990, Shvarts and Demin 1994).

In the present study, type of plant cover seemed to play only small role in habitat niche segregation of shrews in line with other studies showing greater importance of density of plant cover (Terry 1981, Dickman 1995, Casti n and Gos lbez 1999). For example, *N. fodiens* preferred places with denser bushes and herbs than *S. minutus* and *S. coronatus* (Casti n and Gos lbez 1999). And ra (1993, 1995) found that *N. fodiens* was more frequent than *N. anomalus* on stream and river banks with poor vegetation cover. In contrast, *N. anomalus* was more frequent than *N. fodiens* in places with dense cover of hygrophilous plants. Also Ramalhinho (1995) found that *N. anomalus* preferred places with dense vegetation cover. This means that the factor of plant cover density should be included in future investigations of microhabitat preferences of these species.

Most shrew species preferred patches of *Carex* spp. under single trees and hummocks with trees. Possibly, these microhabitats afforded good shelters and nests among tree roots and in crevices between sedge-tussocks and tree trunks.

Distance to the stream and ground wetness appeared to be microhabitat factors of high significance in niche segregation of the species under study. The following

order from the most to the least hydrophilous species was found: *N. fodiens*, *N. anomalus*, *S. minutus* and *S. araneus*. This result is generally consistent with the literature (eg Yudin 1962, Sheftel 1994, Shvarts and Demin 1994) but some dissimilarities should be noted. Ramalhinho (1995) trapped most individuals of *N. anomalus* at considerable distances from water and only a few directly at the edge of rivers or streams, whereas in my study *N. anomalus* was quite frequent within 2 m of the stream. Although *N. fodiens* clearly preferred places 0–0.5 m from the stream, most of captures of this species were recorded at distance > 5 m and some even > 25 m away the stream. This is in contrast to van Bommel and Voesenek (1984) who captured all *N. fodiens* within 0.5 m of the bank edge of peat pits. But it has been reported previously that sometimes *N. fodiens* wanders far from water (Dehnel 1950, Aulak 1970). In my study both *N. fodiens* and *N. anomalus* were similar in preference to places 0–0.5 m from the stream and flooded with > 1 cm of water. However, it has been found in other studies that *N. fodiens* prefers places with access to water > 25 cm deep, fast water flow and steep and diversified banks (Niethammer 1977, 1978, van Bommel and Voesenek 1984, Schröpfer 1985), whereas *N. anomalus* seems to select stream stretches with weak water flow (Niethammer 1977, 1978). Therefore, a detailed analysis of bank structure and water flow may reveal interesting differences between *N. fodiens* and *N. anomalus*.

The mean distances to water were 6.4 m for captures of *N. fodiens*, 7.7 m for *S. minutus* and 12.4 m for *S. araneus* in my study, compared with 9.2 m for *N. fodiens*, 16.6 m for *S. coronatus* (the sibling species to *S. araneus*) and 22.3 m for *S. minutus* in the study of Castián and Gosálbez (1999). The most striking difference between the two studies involves *S. minutus*. In the present study, *S. araneus* preferred much drier ground than *N. fodiens* did, but only slightly drier than *S. minutus*. The same situation was found by Sheftel (1994) in western Siberia. However, in other studies (Yudin 1962, Aulak 1970, Butterfield *et al.* 1981) pigmy shrews preferred wetter places (with muddy or peaty ground) which were avoided by common shrews. Therefore, their microhabitat preferences need further study.

As to the poorly investigated *N. anomalus*, the results obtained suggest that this species prefers places some distance from streams, flooded with shallow or medium water, covered by *Carex* spp., and close to trees. In contrast, *N. fodiens* prefers sites with direct access to streams and deep water. Therefore, the hypothesis on differences in microhabitat preferences of the two *Neomys* species, proposed earlier (Rychlik 1997), cannot be rejected.

The microhabitat differences allowed or obliged the two water shrews to use different foraging modes: wading by *N. anomalus* and diving by *N. fodiens*, which is in accordance with Rychlik's (1997) prediction. *S. araneus* preferred dry ground where it could use epigeal and their preferred hypogeal foraging modes (Churchfield 1994). The microhabitat preferences of *S. minutus* included ground of different wetness and sedge-tussocks where this species could use its epigeal foraging mode (Churchfield 1994). Therefore, also the hypothesis about vertical segregation of foraging microhabitats of the four species cannot be rejected.

Although interspecific differences were not high, the largest shrew, *N. fodiens*, displayed the narrowest habitat niches, the smallest shrew, *S. minutus*, displayed the broadest niches, and the medium-sized species – intermediate niches. [The only exception, the broadest niche of *N. fodiens* with regard to wetness, probably occurred because *N. fodiens* was able to utilise all places, whereas other species were unable to use the wettest places]. This result suggests that *N. fodiens* is a habitat specialist and *S. minutus* is a generalist. Data of other authors (eg Yudin 1962, Sheftel 1994, Churchfield *et al.* 1997) suggest the same. For example, in western Siberia, macrohabitat niche breadth was 0.71 for *N. fodiens* and 1.57 for *S. minutus* (Churchfield *et al.* 1997). In the Pyrenees, microhabitat niche breadths were less differentiated (0.80 for *N. fodiens* and 0.83 for *S. minutus*) but the same tendency was found (Casti n and Gos lbez 1999). Interestingly, trophic niche breadths of these species were in the opposite direction: 3.01 for *N. fodiens* and 2.58 for *S. minutus* (Churchfield 1991b) or 3.72 and 2.92, respectively (Casti n and Gos lbez 1999). Intermediate breadths of trophic niche were found in *S. araneus* (2.67; Churchfield 1991b) and *S. coronatus* (3.69; Casti n and Gos lbez 1999). These facts suggest that an inverse relation may exist between breadths of trophic and habitat niches of shrews: trophic specialists have broad habitat niches, whereas trophic generalists possess narrow habitat niches.

This idea can be justified in the following way: a trophic generalist, which is able to eat variable prey (terrestrial and aquatic, small and large), can satisfy its food requirements within a small area and few habitats. Thus, *N. fodiens*, living along stream banks, has simultaneous access to both aquatic and terrestrial resources and it is not obliged to utilise other habitats. In contrast, a trophic specialist, such as *S. minutus*, is only able to utilise small epigeal prey and has to search for its special food over a larger area and in more different habitats. In fact, *N. fodiens* has a much smaller home ranges (eg Lardet 1988) than *S. minutus* (eg Croin Michielsen 1966). On the other hand, the idea is consistent with the theory that habitat specialists, being superior competitors to generalists, select better habitats and maintain them against generalists (Colwell and Fuentes 1975, Seagle 1985). In the shrew guild that I studied, *N. fodiens* was the largest species and perhaps dominated over the three other species. Thus, it could occupy few optimal microhabitats. However, these relationships need further thorough investigations.

Interspecific similarities

The intergeneric overlaps in macrohabitat preferences were high in the present study and they were even slightly higher than the overlap between *S. araneus* and *S. minutus*. This is in contrast to the situation in Siberia where overlap in macrohabitat preferences between these two *Sorex* species (92.4%) was much higher than the intergeneric overlaps (20.5% for *N. fodiens* vs *S. araneus* and 24.3% for *N. fodiens* vs *S. minutus*; Churchfield *et al.* 1997). This difference may be explained by the possibility that too few and too similar macrohabitats were studied

in my work. However, my results confirm the high similarity of macrohabitat preferences between *S. araneus* and *S. minutus*. On the other hand, the overlaps in microhabitat preferences (highest between *S. araneus* and *S. minutus*, lowest between *N. fodiens* and *S. minutus*, and intermediate between *N. fodiens* and *S. araneus*) resemble those in the equivalent shrew community in the Pyrenees: 74% between *S. coronatus* and *S. minutus*, 53% between *N. fodiens* and *S. minutus*, and 69% between *N. fodiens* and *S. coronatus* (Casti n and Gos lbez 1999).

Throughout the distribution of the Soricidae, wet habitats are the most productive in terms of biomasses and densities of prey and they are inhabited by the highest densities and numbers of coexisting shrew species (Spencer and Pettus 1966, Brown 1967, Wrigley *et al.* 1979, Schr pfer 1990, Kirkland 1991, Shvarts and Demin 1994, Churchfield *et al.* 1997). Therefore, it is possible that my study area included habitats which offered very rich resources and the shrews coexisted under weak competitive interactions. This could explain why the breadths of habitat niches were so similar and the interspecific overlaps in macrohabitat preferences were so high.

Alternatively, strong competition could act among these species, but other mechanisms than differentiation of habitat preferences were also responsible for separation of their ecological niches. This idea is supported by the fact that interspecific overlaps in space distribution of capture were low. Among possible mechanisms are interspecific territoriality (eg Neet 1989), scent and vocal communication (eg Hawes 1976, Krushinska and Rychlik 1993) and differences in activity rhythms (eg Voesenek and van Bommel 1984). Thus, further study is required in both the field and laboratory.

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